

GENERA OF THE BIVALVE FAMILY MESODESMATIDAE, WITH COMMENTS ON SOME AUSTRALASIAN SPECIES

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ABSTRACT

The status of major genus-group names in the Mesodesmatidae is reviewed. Genera recognised in the Subfamily Mesodesmatinae are *Donacilla* de Blainville, 1819, Mediterranean; *Maclropsis* Conrad, 1854, Tertiary of North America; *Atactodea* Dall, 1895, Indo-West Pacific; doubtfully *Ceroniola* Wilckens, 1904, Upper Cretaceous of South America; and *Paphies* Lesson [1831], with subgenera *Paphies* s.str., New Zealand; *Mesodesma* Deshayes [1832], (= *Taria* Gray, 1853), eastern and western South America, and New Zealand; *Amesodesma* Iredale, 1930, south-eastern Australia; and *Ceronia* Gray, 1853, eastern North America. Other generic names in the family are briefly reviewed, and the preoccupied *Nesis* "Monterosato" Locard, 1899, is renamed *Monterosatus*.

Paphies (*Amesodesma*) *perfuga* (Iredale, 1930), type species of *Amesodesma*, is synonymised with *Paphies* (*Amesodesma*) *angusta* (Reeve, 1854). It is suggested that *Mesodesma* *quoyi* Deshayes, [1832] is an earlier name for *Paphies* (*Mesodesma*) *forsteriana* (Finlay, 1927), which in turn is inseparable from *P.* (*Mesodesma*) *pliocenica* (Oliver, 1923).

Myadesma Clark, 1922, seems to belong in the Maclracea, but is placed in the family Myadesmatidae Clark, 1922, rather than in the Mesodesmatidae.

INTRODUCTION

In the latest catalogues of the Bivalvia, Vokes (1967: 268) and Keen (1969: N608) did not list the genus-group name *Amphidesma* in the family Mesodesmatidae Gray, 1840 (= Amphidesmatidae Iredale, 1914, of Australasian workers), but included *Amphidesma* Lamarck, 1818 in the family Semelidae Stoliczka, 1870 (Vokes, 1967: 292; Keen, 1969: N636). Australian and New Zealand workers have been aware for some years that the continued currency of *Amphidesma* was incorrect in the sense of the large, abundant, matracean bivalves so characteristic of sand beaches in New Zealand, but the nomenclature has never been formally stabilised. Dawson (1959) was the first Australasian worker to comment publicly on the situation, while Macpherson and Gabriel (1962) and Garrard (1969) followed Dawson and used *Donacilla* de Blainville, 1819 for the group of small southern Australian shells for which Iredale (1930) provided the genus-group name *Amesodesma*.

Dall (1895a) was the first modern taxonomist to attempt to review generic names in what was then consistently called the Mesodesmatidae. His brief analysis was included in his summary of the classification of the Maclracea, later included in his "new classification of the Pelecypoda" (Dall, 1895b: 556-7) and published in full in Part 4 of his monumental "Tertiary fauna of Florida" (Dall, 1898). Dall's final classification (Dall, 1898: 908-14) is summarised here, with his original statements of type species in most cases. Where comment was thought necessary on dates of publication and on the identity of type species, the original form is given in quotes and the revised one in brackets (not parentheses, which

are Dall's). Dall's synonymising of some names, e.g. of *Erycina* and *Eryx* with *Atactodea*, and of *Amphidesma* with *Mesodesma*, is a synonymising of generic concepts, and has not been followed in the present paper. Dall (1900: 985) later formally synonymised *Amphidesma* with *Semele*, using an invalid "selection" by Bowdich of *Amphidesma variegata* as type.

Family Mesodesmatidae

Subfamily Mesodesmatinae

Genus *Mactropsis* Conrad, 1854 (nom. nov. for *Triquetra* Conrad, 1846, non de Blainville, 1818); type *M. aequorea* Conrad, Eocene, North America.

Genus *Atactodea* Dall, 1895 (= *Paphia* Lamarck, 1799, non Röding, 1798; = *Erycina* Sowerby, 1822, non Lamarck, 1805; = *Eryx* Swainson, 1840, non Daudin, 1832, nec Stevens, 1833, Insecta); type, "*Paphia glabrata* (Lam.), Indo-Pacific region" [= *Mactra glabrata* Gmelin [1791], despite Dall's statement to the contrary].

Genus *Mesodesma* Deshayes, "1830" [1832]. Subgenus *Mesodesma* s.str. (= *Ceronia* Gray, 1853); type, *M. donacium* (Lamarck) (+ *M. chilense* Orb.); Chile. Subgenus *Donacilla* Philippi, 1836 (= *Amphidesma* Lamarck, 1818); type *M. corneum* (Poli); Mediterranean. Subgenus *Taria* Gray, 1853; type, *M. stokesii* Gray (MS.?) = *M. latum* Desh., New Zealand. Subgenus *Paphies* Lesson, "1830" [1831] (= *Machaena* (Leach MS.) Gray, 1823); type *Mya australis* Gmel. (= *Mya novaezelandiae* Chemnitz, *Paphies Roissyana* Lesson, et *Mesodesma* Chemnitzii Deshayes); New Zealand.

Subfamily Davilinae Dall, 1895

Genus *Davila* Gray, 1853; type *D. polita* Gray (MS.?) = *D. plana* Hanley, [Indo-Pacific].

Genus *Anapella* Dall, 1895 (= *Anapa* Gray, 1853, non Gray, 1847); type, *Anapa Smithii* Gray, = *A. triquetra* Hanley, Tasmania.

Subfamily Erviliinae Dall, 1895

Genus *Coecella* Gray, 1853; type, *C. Horsfieldii* Gray (MS.?): China.

Genus *Ervilia* Turton, 1822; type, *Mya nitens* Montagu; Britain, South Europe.

The only generic names listed by Vokes (1967) that are not included in Dall's classification are many incorrect subsequent spellings (not considered in this paper), *Nesis* "Monterosato, 1875" (*nomen nudum*) Locard, 1899, four times preoccupied and apparently never renamed; and the four later-erected names *Argyrodonax* Dall, 1911; *Rochefortina* Dall, 1924; *Amesodesma* Iredale, 1930; and *Spondervilia* Iredale, 1930. Keen (1969: N608, N610) has recently included *Ceroniola* Wilckens, 1904 and *Myadesma* Clark, 1922 in the family. These, the genera of the Davilinae and Erviliinae, and *Mactropsis* Conrad, *Atactodea* Dall, and *Ceroniola* Wilckens will be

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considered briefly later; the main purpose of the paper is to evaluate the generic names of the *Mesodesma-Donacilla* complex.

Iredale and McMichael (1962: 26) placed *Benthoquetia* Iredale, 1930 (June 27th) in the "Amphidesmatidae", but there is no justification for such a position. Iredale (1930: 403) placed the genus in the Family Myacidae (sic), whereas Cotton (July 18th, 1930: 239) placed the absolute synonym *Austroturquetia* (= *Auroquetia* Ponder, 1968, incorrect subsequent spelling), by inference, in the same family as *Turquetia* Velain (currently in the Galeommadiata). Vokes (1967: 250) placed the genus in the Montacutidae; Chavan (1969: N541) placed it in the Sportellidae, as a sub-genus of *Isoconcha* Dautzenberg and Fischer; and Ponder (1968: 129) showed that on anatomical features "the Montacutidae is a likely position".

Attempts after that of Dall to classify the family in Australia and New Zealand led to highly incorrect conclusions. Suter (1913) followed Dall. Iredale (1914) tried to rectify Suter's nomenclature, but considered the type species of *Amphidesma* to be "*Donacilla*" *donacilla* Lamarck by tautonymy, as *Amphidesma* was Lamarck's Latin name for his vernacular "Donacille".

An application has been made to the International Commission on Zoological Nomenclature (Beu, 1971), to have *Amphidesma variegata* Lamarck, 1818 (= *Tellina purpurascens* Gmelin, [1791]), selected by subsequent designation of Children (1823: 301), confirmed as type-species of *Amphidesma* Lamarck, 1818; and to have *Donacilla lamarckii* Philippi, 1836, selected by subsequent monotypy of Philippi (1836: 37), confirmed as type-species of *Donacilla* de Blainville, 1819. If the requests are granted, this will have the effect of making *Amphidesma* a junior subjective synonym of *Semele* Schumacher, 1817, and of using *Donacilla* (attributed to de Blainville, 1819: 429) in its place in the Mesodesmatidae. This paper is written as though the requests has been granted, since the results are the current majority opinion; the name *Amphidesma* need not be considered further.

Finlay (1927: 467-9) followed Iredale's generic nomenclature, and as Finlay's large paper has been regarded until recent years as the "starting point" in New Zealand molluscan taxonomy, the generic nomenclature has not been questioned. Thus all Powell's lists of New Zealand Mollusca (e.g. Powell, 1962) and Fleming's (1966) list of New Zealand Cenozoic Mollusca continued to use the names *Amphidesma* and Amphidesmatidae.

Dawson (1959) arrived at very different conclusions from either Dall (1895a; 1895b; 1898) or Iredale (1914), pointing out the type-designation for *Amphidesma* by Children. He concluded that *Donacilla* de Blainville, 1819 should be used instead of either *Amphidesma* or *Mesodesma*, for a mesodesmatid genus. Dawson's work has unaccountably received little attention in New Zealand. An attempt has been made here to evaluate the genera from both a nomenclatural viewpoint and the conchological characters of their included species.

Combined Descriptions of Genera and Species

Gray (1853) gave succinct diagnoses of five new genera of Mesodesmatidae (one of them, *Coecella*, in the preceding Mactridae), and included a single species in each genus. One of the species, in *Ceronia*, he had named previously, so that this is the type species by monotypy, and all is clear. In the cases of *Coecella*, *Anapa*, *Davila* and *Taria* the species

names had not been published in earlier works, and no description or definition was given for any of them. My first instinct was to regard the included species as *nomina nuda*, and the four generic names thus as *genera caelibes*, and to seek the first subsequent placing of species in them (and subsequent designation of a type, if the two were different). However, I now regard these cases as joint descriptions of genera and species (Code, Article 16 (a) vi). There is a subtle (but important) difference between a new generic name followed by the description of a new genus and species, and the description of a new genus followed by a new specific name; but the Code does not distinguish between the two, and the names erected by Gray (1853) appear to fall under Article 16 (a) vi. The alternative results that would obtain if this conclusion is not accepted are given under each of the relevant generic headings.

TAXONOMY

Family Mesodesmatidae Gray, 1840

As was pointed out to me by Professor Keen (*in litt.*, January 22, 1970), in the *Treatise on Invertebrate Paleontology* review of Mesodesmatidae (Keen, 1969: N608) the name Mesodesmatidae was attributed to Gray, 1839, but the subfamily Mesodesmatinae was attributed to Gray, 1840. The reference intended for both by Keen is that of Gray (1840: 149). Vokes (1967: 278) attributed the name to Deshayes, 1839, but a reference to this name cannot be found (Prof. H. E. Vokes, *in litt.*; Prof. A. Myra Keen, *in litt.*). Determining the first publication and author of family-group names is very difficult, and its value appears slight.

Subfamily Mesodesmatinae

Genus *Donacilla* de Blainville, 1819

1819. *Donacilla* de Blainville, *Dictionnaire des Sciences Naturelles*, 13: 429. Type species (by subsequent monotypy, Philippi, 1836): *Donacilla tamarckii* Philippi, 1836 (= *Amphidesma donacilla* Lamarck, 1818, = *Mactra cornea* Poli, 1795), Recent, Mediterranean (I.C.Z.N. opinion pending).

Dawson (1959: 44) treated *Donacilla* de Blainville, 1819 (de Blainville, 1819: 429) as an available name, but most recent authors have attributed it to Philippi (1836: 37). Vokes (1967: 278) considered *Donacilla* de Blainville to be a *nomen nudum*, but it is not, as de Blainville (cited in full by Dawson, 1959: 44; and earlier by Iredale, 1914: 490) gave a bibliographic reference to Lamarck's description of *Amphidesma* (Lamarck, 1818: 489), which constitutes an indication under Article 16 (a) i. Possible consideration of *Donacilla* to have been published in synonymy because of the cited description of *Amphidesma* (e.g. by Keen, 1969: N609) is incorrect, since it was used as an available name for a taxon by Dawson, and earlier by Philippi (1836: 37) (Article 11d). An application to the International Commission on Zoological Nomenclature (Beu, 1971; discussed above) will have the effect of ratifying the present usage of *Donacilla* in place of *Amphidesma* in the Mesodesmatidae, attributing *Donacilla* to de Blainville, and reducing *Amphidesma* to a synonym of *Semele* Schumacher, 1817, if granted. Since this is the current majority usage, this paper is written as if the requests to the Commission had been granted.

"*Donacina* Blainville, 1818" was listed as a generic name (but as an error for *Donacilla* Lamarck, 1819 [sic]) by Neave (1939: 143). The only

place where a word resembling the Latinised *Donacina* appears in de Blainville (1818) is in a fold-out table of classification of Mollusca, following p. 216; all generic names on the table are French vernacular *nomina nuda*. The word "Donacine" appears on the eighth line of examples from the bottom of the table. Thus the name *Donacina* does not date from de Blainville (1818).

The hinge of *Donacilla cornea* (Poli), apparently the sole living species to be included in the genus, is unique in the Mesodesmatidae in having a very narrow, insignificant resilifer, and in having large, well-developed cardinal teeth (see Fig. 10); in all other Mesodesmatidae the cardinal teeth are greatly reduced or absent. Thus *Donocilla* seems best treated as a full genus, and another name must be used for most large species of Mesodesmatidae.

Genus *Paphies* Lesson, [1831]

[1831]. *Paphies* Lesson, in Lesson and Garnot, *Voyage Autour du Monde . . . sur . . . La Coquille . . .*, *Zoologie*, 2 (1): 424. Type species (by monotypy): *Paphies* (*Crassatella*) *roissyana* Lesson, 1831 (= *Mya australis* Gmelin, [1791]), Pliocene to Recent, New Zealand.

The figures of *Paphies roissyana* given by Lesson (in Lesson and Garnot, 1826-[31], Atlas, pl. 15, figs. 4, 4a) are beautifully accurate, natural-size, coloured illustrations of the common New Zealand "pipi", long known as *Amphidesma australe* (Gmelin). The species is rendered highly distinctive in the Mesodesmatidae by its elongate form with central umbones, and by its prominent but short, only slightly oblique lateral teeth. Apart from the differences in shell shape (which presumably reflect a significantly different anatomy), and relatively minor differences in the hinge, the species is very similar to species of *Mesodesma* (as interpreted here), and the two groups seem best ranked as subgenera. As *Paphies* Lesson was proposed in December 1831 (Sherborn and Woodward, 1906a) whereas *Mesodesma* Deshayes was not proposed until 1832 (Sherborn and Woodward, 1906b), *Paphies* must become the nominate subgenus.

The generic name *Machaena* "Leach" J. E. Gray (Gray, 1843: 252) and the included species *M. ovata* Leach and *M. subtriangulata* (presumably *Maetra subtriangulata* Wood) were all published in the synonymy of *Mesodesma chemnitzii* Deshayes, [1832] (= *Mya australis* Gmelin, [1791]) and have never been used as available generic names. Thus they are unavailable under Article 16 (b).

The subgenus *Paphies* (s.str.) is represented by only three named forms, *P. anteaustralis* (Dell, 1950) from the Lower Miocene of New Zealand, *P. australis australis* (Gmelin, [1791]) from the Pliocene to Recent of mainland New Zealand, and the doubtful subspecies *P. australis aucklandica* (von Martens, 1879) from the Auckland Islands.

The interior of a right valve of *Paphies* (s.str.) *australis* is figured as Fig. 8.

Subgenus *Mesodesma* Deshayes, [1832]

[1832]. *Mesodesma* Deshayes, *Encyclopédie Méthodique*, Vers, 2 (2): 441. Type species (by subsequent designation, Anton, 1839): *Mesodesma donacium* Deshayes, [1832] (= *Maetra donacia* Lamarck, 1818), Recent, Chile and Peru.

1853. *Taria* J. E. Gray, *Ann. Mag. Nat. Hist.*, (2), 11: 44. Type species (by monotypy): *Taria stokesii* Gray, 1853 (= *Maetra subtriangulata* Wood, 1828), Recent, New Zealand.

Herrmannsen (1847: 40), Gray (1847: 186) and Gray (1853: 44) all designated *Mya Novae Zelandiae* Chemnitz (sometimes subsequently

written *M. novaezealandiae*) as type species of *Mesodesma*, but this is not only an unavailable non-binominal name, but also was not among the species originally included in *Mesodesma* by Deshayes (1832: 442-4). Thus the designation by Dall (1895a: 213) of *Mesodesma donacium* Lamarck as type species of *Mesodesma* has generally been accepted as the first valid one. However, as shown by Keen (1969: N608), Anton (1839: 3) had much earlier validly designated the same species as type.

H. and A. Adams (1856: 413) were the first after Gray to use *Taria*; they included *Mesodesma latum* Deshayes and *M. spissum* Reeve, without designating a type species. Both of these species are available for designation as type species of *Taria* (Article 69 (a) ii), if *stokesii* is not accepted. Dall (1898: 912) stated: "Subgenus *Taria* Gray . . . Type *M. stokesii* Gray (MS.?) = *M. latum* Desh., N. Zealand". This would constitute designation of the available synonym, *Mesodesma latum* Deshayes, 1843, as type species of *Taria* Gray (Article 69 (a) iv), if my conclusions on combined genus and species descriptions are not accepted.

South American species, particularly *Paphies* (*Mesodesma*) *donacia* (Lamarck) (Fig. 1), differ from New Zealand species such as *P. ventricosa* (Gray, 1843) (Fig. 2) and *P. subtriangulata* (Wood, 1828) (type species of *Taria* Gray, 1853) and, in particular, from *P. subtriangulata porrecta* (Marwick, 1928), (Fig. 6), in only minor specific features, and I can see no reason for maintaining *Taria* as a separate genus-group from *Mesodesma*. Figures of interiors and hinges of several species are given (Figs. 1-3, 6-9) to support this contention. All South American and New Zealand species have smooth lateral teeth.

The status of some New Zealand forms of *Paphies* (*Mesodesma*) calls for comment (Deshayes' types must be examined before a detailed revision can be carried out). Firstly, most recent authors have quoted the Latin name of the common "tuatua" as "*Amphidesma*" *subtriangulatum* (Wood, 1828), whereas Suter (1913: 957), Lamy (1914: 22) and Dawson (1959: 45) quote *Mesodesma* (or *Donacilla*) *subtriangulatum* (Gray, 1825). Iredale (1914: 491) long ago cleared this point up by giving a full quotation from Gray (1825, *Ann. Philos.*, 35, p. 135; not seen by me): "*Ery(cina) subangulata*. *Crassatella cuneata* Lam., 483?". Iredale (1914: 491) commented: "Note the spelling of the specific name, and, as the above is the complete entry, it is quite obvious that it is a *nomen nudum*". If Iredale's quotation from Gray is correct, the name *Erycina subangulata* Gray, 1825 is a synonym of the synonymised available name *Crassatella cuneata* Lamarck, 1818, which applies to a small southern Australian species of *Paphies* (*Amesodesma*). In the same work Iredale (1914: footnote to p. 491) stated that Lamy's work showed that the next available name is *Mactra subtriangulata* Wood, 1828.

Secondly, Iredale again seems to have been more correct on a point of nomenclature than later workers gave him credit for. On p. 492 he used "*Amphidesma quoyi* (Deshayes)" as a good New Zealand species, noting that Deshayes' type specimen had a "flattened" posterior slope, whereas *A. gaimardi* [sic] (Deshayes) and *A. ventricosum* (Gray) have bicarinate posterior slopes. From this description and from Lamy's (1914: 24, fig. 1) sketch of the type of *Mesodesma quoyi* Deshayes, it seems very likely that this is the form later named *Amphidesma plioceni-*

cum by Oliver (1923: 187) and *Amphidesma forsterianum* by Finlay (1927: 468). Finlay stated that all named forms were based on "northern" shells, and could not be the form he named *forsterianum*, but I know of no evidence to support his statement. The status of the form here called *quoyi*, compared with that of *P. subtriangulata* (Wood), is greatly in doubt. Dawson (1959) regarded it as a recognisable southern subspecies of *subtriangulata*, suggesting the name *pliocenica* be used for it. Certainly *pliocenica* Oliver and *forsteriana* Finlay are not sufficiently different to be maintained as separate subspecies, whatever their status compared with those of *quoyi* and *subtriangulata*. In my opinion *P. "pliocenica"* is a valid southern subspecies of *P. subtriangulata*, having a broad zone of overlap in the Wanganui-Christchurch region, but it seems likely that *Mesodesma quoyi* Deshayes will prove to be the earliest name for it. I tentatively list the named New Zealand forms of *Paphies* (*Mesodesma*) as follows:

- P. crassiformis* (Marshall and Murdoch, 1920), Pleistocene; Fig. 9;
- P. subtriangulata subtriangulata* (Wood, 1828) [= *gaymardi* Deshayes, [1832] = *spissa* Reeve, 1854], Pleistocene to Recent; Recent in northern New Zealand; Fig. 3;
- P. subtriangulata quoyi* (Deshayes, [1832] [= *lata* Deshayes, 1843 = *pliocenica* Oliver, 1923 = *forsteriana* Finlay, 1927], Pliocene to Recent; Recent in southern New Zealand; Fig. 7;
- P. subtriangulata porrecta* (Marwick, 1928), Pleistocene to Recent, Chatham Island; Fig. 6;
- P. ventricosa* (Gray, 1843), Pleistocene to Recent; Recent throughout mainland New Zealand; Fig. 2.

Subgenus *Amesodesma* Iredale, 1930

1930. *Amesodesma* Iredale, *Rec. Aust. Mus.*, 17: 402. Type species (by original designation): *Amesodesma perfuga* Iredale, 1930 (= *Mesodesma angustum* Reeve, 1854), Recent, south-eastern Australia.

Garrard (1969: 7) regarded *Amesodesma* as not validly introduced, and placed New South Wales species in *Donacilla* de Blainville, following Macpherson and Gabriel (1962: 360), who in turn were following Dawson (1959). Garrard stated that the name was associated only with the new subspecies *Amesodesma cuneatum vanadicum* Iredale, but in a much fuller description Iredale established "*Amesodesma perfuga* n.sp." on the same page as *A. cuneatum vanadicum*. The genus-group name *Amesodesma* is quite validly introduced under Article 12, and in the paper in which it was introduced, Iredale (1930: 407) designated *Amesodesma perfugum* Iredale as type species of the genus-group.

The type species of *Amesodesma* has a highly unusual resiliifer, which is relatively long and inclined at a high angle to the normal vertical position, directed strongly towards the anterior end of the shell, and projecting prominently below the hinge line at its posterior end. The muscle scars are as in *Mesodesma*, and the pallial sinus is of medium depth. However, the siphons of preserved specimens of *Paphies* (*Amesodesma*) *angusta* (Reeve) examined in the Australian Museum during August 1969, with the help of Dr W. F. Ponder, were extremely short for the genus-group, being about 2 mm long in a shell about 20 mm long. The hinges of the other south-eastern Australian species of "*Mesodesma*"

examined in the Australian Museum (notably *cuneata* Lamarck, 1818, common in Victoria and New South Wales) have vertical resilifers that project only moderately below the hinge line; their hinges are otherwise similar but their relative siphon length has not been seen. Thus hinge differences are too minor to be used to separate *Amesodesma* from *Mesodesma*, but it seems likely that species placed in *Amesodesma* have shorter siphons than those of *Mesodesma*. The group is separable also by its consistently very small size; individuals of *Paphies angusta* and *P. cuneata* rarely reach more than 25 mm in length, whereas *P. (Mesodesma) donacia* (Lamarck) is frequently more than 100 mm long, and *P. (Mesodesma) ventricosa* (Gray) is commonly over 200 mm in length and reaches over 300 mm. Judged by the small percentage of bivalves having trans-Tasman relationships, trans-Tasman dispersal of bivalves is rare, and the group of small Australian shells seems likely to have had a long geological history separate from that of *Mesodesma* (as here interpreted). In my opinion the Australian group is worthy of recognition as the subgenus *Amesodesma*. Interiors of right valves of *Paphies (Amesodesma) angusta* (Fig. 5) and *P. cuneata* (Fig. 4) are figured here.

Specimens examined in the Australian Museum during August 1969 show that *Paphies (Amesodesma) perfuga* (Iredale) cannot consistently be separated from *P. angusta* (Reeve). The type series of *perfuga*, from Gunnamatta Bay, Port Hacking, N.S.W., consisting of 35 single valves plus the holotype, is consistent in having a slightly longer posterior end than in typical *P. angusta*, but is the only such population known to me. Populations with end members resembling both Reeve's figure of *P. angusta* and the holotype of *P. perfuga* were seen from: C13017, Stradbroke Id., Queensland, coll. C. Hedley; C50912, Flat Rock, north of Richmond River, N.S.W., coll. A. O'Sullivan; C69072, Jervis Bay, N.S.W., coll. W. F. Ponder; Shoal Bay, Port Stephens, N.S.W., coll. G. P. Whitley; Gunnamatta Bay, Port Hacking, N.S.W., coll. T. A. Garrard (topotypes of *P. perfuga*, but only one specimen in the collection of 14 resembles the holotype of *perfuga*). There can be no doubt that *P. perfuga* (Iredale) is based on specimens of *P. angusta* with slightly longer posterior ends than usual, and the two names are here synonymised.

Subgenus *Ceronia* Gray, 1853

1853. *Ceronia* J. E. Gray, *Ann. Mag. Nat. Hist.*, (2), 11: 44. Type species (by monotypy): *Ceronia denticulata* (= *Erycina denticulata* Gray, 1825 = *Mesodesma deauratum* Turton, 1822), Recent, Gulf of St Lawrence.

The commonly-accepted synonymy of *Ceronia* Gray with *Mesodesma* Deshayes seems to me to be incorrect. Davis (1965: pl. 9) figured the holotype of *Mesodesma deauratum* Turton, type species of *Ceronia*, and noted that it is a common, in some places abundant, species in the St Lawrence estuary and the Gulf of St Lawrence. Superficially the figured shell closely resembles *Paphies* (s.str.) *australis* (Gmelin), but closer comparison shows that the pallial sinus is much shorter and more angular, the outer anterior lateral tooth is very much shorter and more steeply inclined, all lateral teeth protrude further and are smooth (transversely ridged in *P. deaurata*), the resilifer is narrower, and the posterior end of the shell is slightly longer in *P. australis* than in *P. deaurata*. The lectotype of *P. arctata* (Conrad), figured earlier by Davis (1964: pl. 4), has rigid lateral teeth similar to those of *P. deaurata*, but is not quite as elongate posteriorly. Figures of the hinge of *P. arctata* given by Davis (1967: pl. 1,

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figs. 1, 2) show the ridged lateral teeth clearly. The group of eastern North American species of *Paphies* is considered to warrant separation from *Mesodesma* because of its rigid lateral teeth and elongate posterior end of the shell. The name *Ceronia* Gray, 1853 is available for the group.

The subgenus has a fossil history from the Oligocene in eastern North America (Dall, 1898: 912). *Paphies* (*Mesodesma*) *donacia* is known fossil in the Tertiary (late Pliocene and above; Herm, 1969: 94) of Chile, whereas no species of *Paphies* (sensu lato) are known in the Tertiary of Patagonia (von Ihering, 1907: 522). This suggests that *Mesodesma* is a recent immigrant to the east coast of South America, apparently from the west coast. There can be little doubt that *Ceronia* and *Mesodesma* are phylogenetically separate groups.

OTHER GENERA OF THE MESODESMATIDAE

To fill out the bald statements of Dall's (1898) catalogue, from which the status of many names cannot be determined in detail, and to clarify some minor errors in the Bivalvia volume of the *Treatise* (Keen, 1969), a list is given here of the recognised genera of the Mesodesmatidae that have not been discussed above. Nomenclatural comments are appended where necessary. Nomenclatural data are based on Lamy's (1914) excellent review of the family to which readers are referred for figures and descriptions of almost all known species.

Subfamily Mesodesmatinae

Genus *Atactodea* Dall, 1895

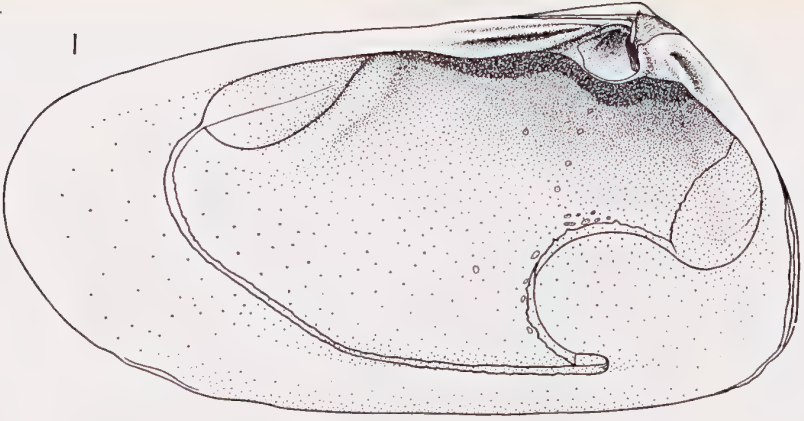
1799. *Paphia* Lamarck, *Mem. Soc. Hist. Nat. Paris*, (1), 1: 85 (genus *caelebs*) (non Röding, 1798, Mollusca). Type species (by subsequent designation, Gray 1847): *Maetra glabrata* Gmelin [1791] (? = *Maetra striata* Gmelin, [1791]), Recent, indo-West Pacific.
1895. *Atactodea* Dall, *Proc. Malac. Soc. Lond.*, 1: 213. New name for *Paphia* Lamarck, 1799, non Röding, 1798.

Keen (1969: N608) indicated that the type species of *Paphia* Lamarck was selected by original designation. However, Lamarck (1799: 85) did not include a species name beneath the description of the new genus *Paphia*, as he did with almost all other generic names in his "Prodrome d'une nouvelle classification des coquilles". The description given by Lamarck includes a clear description of the mesodesmatid hinge: ". . . fossette du ligament située sous les crochets entre les dents de la charnière, . . .", so that *Paphia* is available under the Code, Article 12, and is a genus *caelebs* where proposed. The first designation of a type seems to be the quoted one by Gray (1847). Dall (1895; 1889) included *Erycina* "Sowerby, 1822" and *Eryx* Swainson, 1840 in the synonymy of *Atactodea*. In the first of these references, J. Sowerby and G. B. Sowerby 1st (1822) included three species of Mesodesmatidae [*Paphies* (*Amesodesma*) *cuneata* (Lamarck), *Atactodea striata* (Gmelin), and an unidentifiable species, possibly *Donacilla cornea* (Poli)] in *Erycina*, which in concept is thus not *Erycina* in the sense of Lamarck. However, Dall was

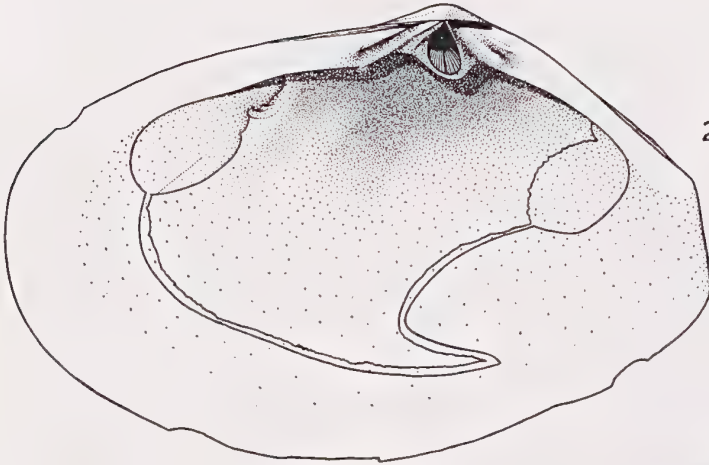
Figures 1 - 5. Right valves of *Paphies*. 1, *Paphies* (*Mesodesma*) *donacia* (Lamarck), type species of *Mesodesma* Deshayes; Chepu, west coast of Chiloe Id., Chile; N.Z. Geological Survey, WM7694. 2, *Paphies* (*Mesodesma*) *ventricosum* (Gray); Muriwai Beach, Auckland, New Zealand; N.Z. Geological Survey, RM2759. 3, *Paphies* (*Mesodesma*) *subtriangulata* *subtriangulata* (Wood), type species of *Tartia* Gray; Ohope Beach, Whakatane, New Zealand; N.Z. Geological Survey, RM2907. 4, *Paphies* (*Amesodesma*) *cuneata* (Lamarck), Tasmania; N.Z. Geological Survey, WM9716. 5, *Paphies* (*Amesodesma*) *angusta* (Reeve); paratype of *Amesodesma* *perfulgum* Iredale, type species of *Amesodesma*; Gunnamatta Bay, Port Hacking, New South Wales; Dominion Museum, MF21733.

Figs. 1 - 3 approx. natural size; figs. 4, 5 enlarged approx. X 2.

1



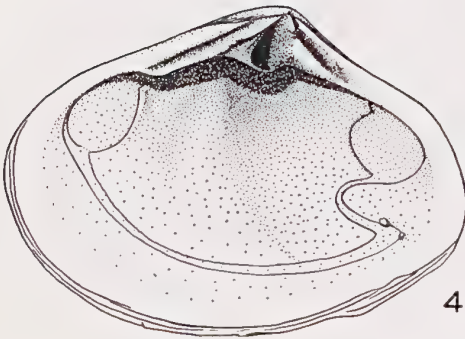
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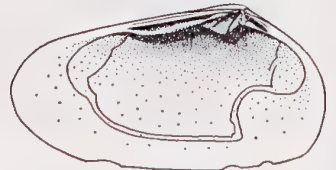
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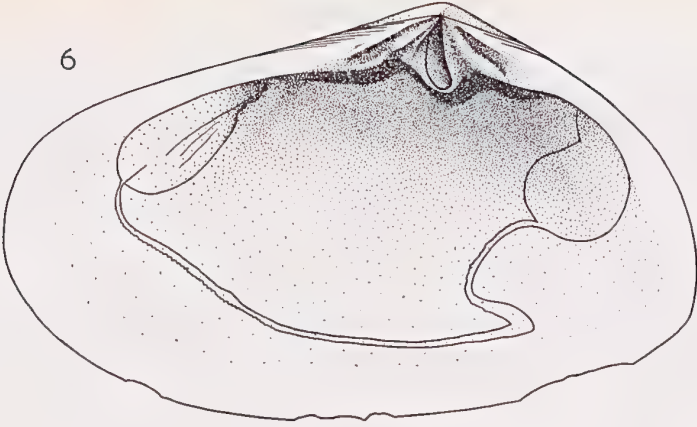
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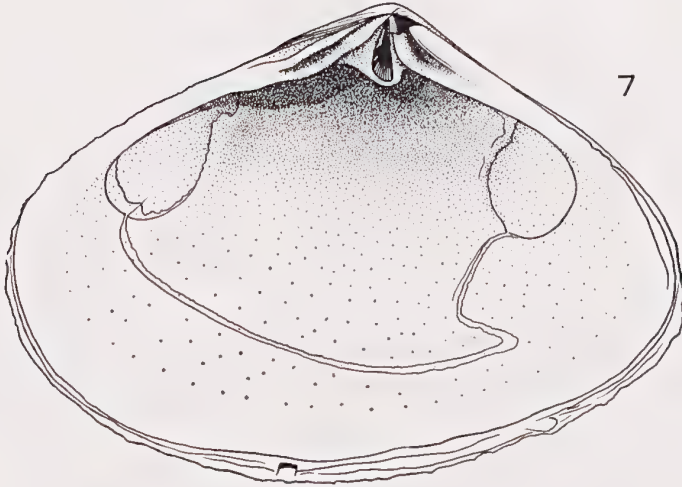
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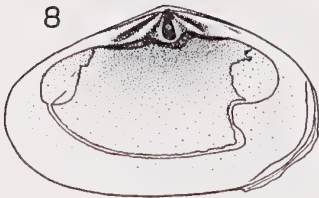
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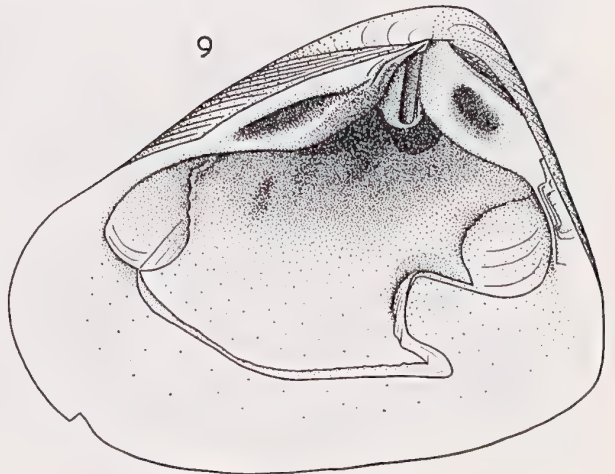
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10



only synonymising the generic concepts, and this name and *Eryx* are not synonyms of *Paphia*. Swainson (1840: 370, footnote) stated clearly that he was proposing the new name *Eryx* to replace *Erycina* Lamarck, which he believed to be preoccupied by a name proposed in Insecta by Fabricius. Thus *Eryx* Swainson is a junior objective synonym of *Erycina* Lamarck (it was so treated by Vokes, 1967: 248; Chavan, 1969: N519), regardless of what species Swainson included in *Eryx* (he actually included what appears to be *Atactodea striata*; Swainson, 1840: 368, figs. 118, d, e).

Atactodea is the abundant, small, relatively strongly concentrically ribbed mesodesmatid of atoll lagoons throughout the Indo-West Pacific. *Davila*, occurring in the same area and habitat, is readily distinguished by its smooth, rounded form, slight inflation, and almost complete absence of a pallial sinus.

Genus *Mactropsis* Conrad, 1854

1846. *Triquetra* Conrad, *Am. J. Sci.* (2), 1: 217 (non de Blainville, 1828, Mollusca). Type species (by subsequent designation, Dall, 1895a): *Erycina aequorea* Conrad, 1833, Middle Eocene, Alabama.
1854. *Mactropsis* Conrad, *Proc. Acad. Nat. Sci. Philad.*, 7: 30. New name for *Triquetra* Conrad, 1846, non de Blainville, 1828.

Dall (1898: 910-11) presented evidence for considering *Mactropsis* as a primitive mesodesmatid, rather than as a mactrid. For this reason the genus is retained here. Palmer and Brann (1965: 190) placed *Mactropsis* in the Mactridae, whereas Keen (1969: N610) retained it in the Mesodesmatidae.

? Genus *Ceroniola* Wilckens, 1904

1904. *Ceroniola* Wilckens, *Neues Jb. Min. Geol. Paläont., Beil.*, 18: 249. Type species (by monotypy): *Cultellus australis* Gabb, 1860, Upper Cretaceous, Chile.

This genus, included in the Cultellidae by Vokes (1967: 280), was tentatively included in the Mesodesmatinae by Keen (1969: N608). Wilckens (1904: 250-1) was most emphatic that the genus belongs in the Mesodesmatidae in spite of its unusual hinge, interpreted by him as having the resilium triangular, small, and attached behind a small, oblique, forward-directed tooth protruding below the beaks. The lateral teeth are well developed and show clearly in Wilckens' (1904: pl. 20, fig. 11a, b) figures, copied clearly by Keen (1969: fig. E101, 8a-c). Wilckens thought the hinge was perhaps slightly damaged during preparation, and did not have a perfect example among approximately 50 specimens. If the resilium is correctly interpreted the genus must be placed in the Mactracea, but the details may rule out its inclusion in the Mesodesmatidae. It is here tentatively retained in the Mesodesmatidae for want of a better position.

Wilckens (1904) recorded *Ceroniola australis* (Gabb), the sole species, only from the Quiriquina beds (Campanian-Maastrichtian) of Chile, suggesting it was an ancestor of "*Ceronia*" [in his sense, *Ceronia* = *Meso-*

Figures 6 - 10. Right valves of Mesodesmatidae. 6, *Paphies* (*Mesodesma*) *subtriangulata porrecta* (Marwick), holotype; GS1178, Titirangi, Chatham Is. (Nukumaruan, early Pleistocene); N.Z. Geological Survey, TM4738. 7, *Paphies* (*Mesodesma*) *subtriangulata quoyi* (Deshayes); Kartigi Beach, Dunedin, New Zealand; N.Z. Geological Survey, TM4974. 8, *Paphies* (s.str.) *australis australis* (Gmelin), type species of *Paphies* Lesson; Petone Beach, Wellington Harbour, New Zealand; N.Z. Geological Survey, RM1313. 9, *Paphies* (*Mesodesma*) *crassiformis* (Marshall and Murdoch), holotype; Nukumaruan Beach, Wanganui, New Zealand (Nukumaruan, early Pleistocene); N.Z. Geological Survey, TM4736. 10, *Donacilla cornea* (Poli), type species of *Donacilla* de Blainville; Toulon, France, C. Cooper Colln.; Auckland Institute and Museum, AM24945.

Figs. 6 - 9 approx. natural size; fig. 10 enlarged approx. X 2.

Mesodesmatidae

desma of this paper]. A much more likely ancestor of the Mesodesmatidae, with a considerably more generalised shape and a more typical mactracean hinge, is *Mactropsis* Conrad from the Eocene of North America. This evolutionary relationship supports the view that *Cerioniola* is not a mesodesmatid. Keen's (1969: N608) statement that *Cerioniola australis* is of upper Tertiary age is presumably an error for Upper Cretaceous.

Subfamily Davilinae Dall, 1895

The usefulness of the subfamilies erected by Dall (1895a) is open to considerable doubt. He separated *Anapella* and *Davila* from the Mesodesmatinae by their absence of a pallial sinus, but a very small posterior inflection of the pallial line is present in both genera, immediately in front of the posterior adductor muscle scar. Anatomical examination will show the validity or otherwise of Dall's groups, which are tentatively maintained in this primarily nomenclatural review.

Genus *Anapella* Dall, 1895

1853. *Anapa* J. E. Gray, *Ann. Mag. Nat. Hist.*, (2), 11: 44 (not *Anapa* Gray, 1847, = *Lasaea*). Type species (by monotypy): *Anapa smithii* Gray, 1853 (= *Mesodesma triquetrum* Hanley, 1843, = *Amphidesma cycladeum* Lamarck, 1818), Recent, south-eastern Australia.
1895. *Anapella* Dall, *Proc. Malac. Soc. Lond.*, 1: 213. New name for *Anapa* Gray, 1853, non Gray, 1847.

Macpherson and Gabriel (1962: 359) pointed out that the earliest name for the type species of *Anapella* is *Amphidesma cycladeum* Lamarck, 1818. *Anapella cycladea* is a readily recognisable, strongly inflated, weakly concentrically sculptured, prominently toothed species occurring in Tasmania and south-eastern Australia. It appears to me to be related to *Paphies* (s.lat.) rather than to *Davila*, and thus the Davilinae is probably heterogeneous.

If my conclusions on combined genus and species descriptions are not accepted, Dall's (1895a: 213) statement that the type species of *Anapella* is "*Anapa triquetra*, Hanley" would constitute subsequent designation of that species as type.

Genus *Davila* Gray, 1853

1853. *Davila* J. E. Gray, *Ann. Mag. Nat. Hist.*, (2), 11: 44. Type species (by monotypy): *Davila polita* Gray, 1853 (= *Mesodesma planum* Hanley, 1843), Recent, Indo-West Pacific.

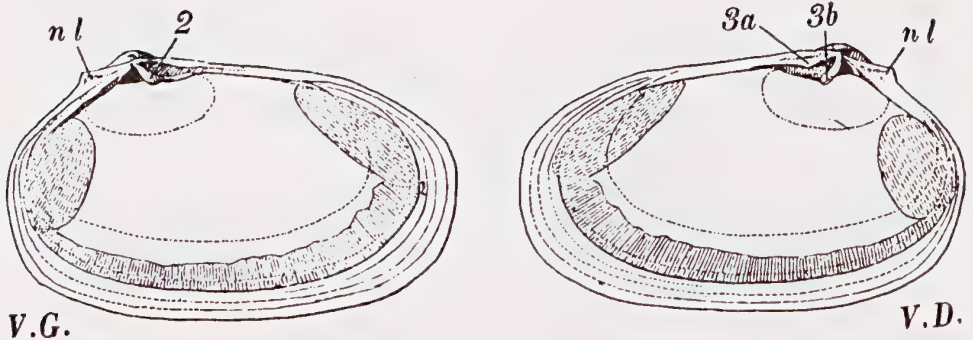
The statement by Dall (1898) that the type species of *Davila* was "*D. polita* Gray (MS.?) = *D. plana* Hanley" would constitute designation of the synonymised available species as type species of *Davila* if my conclusions on combined genus and species description are not accepted.

Davila plana, with its smooth, polished exterior, its slight inflation, its heavy hinge plate, and its very small posterior inflection in the pallial line, is one of the most easily recognised members of the family. It occurs commonly in atoll lagoons throughout the Indo-West Pacific.

Genus *Monterosatus* nom. nov.

1875. *Nesis* Monterosato, *Atti Accad. Palermo*, (2), 5: 4 (*nomen nudum*).
1899. *Nesis* Locard, *Les coquilles marines au large des côtes de France*: 155. Type species (by monotypy): *Nesis prima* "Monterosato" Locard, 1899, Recent, Mediterranean. [Non *Nesis* Mulsant, 1850. Coleoptera; nec Stal, 1869, Hemiptera; nec Conrad, 1871, Mollusca; nec Cambridge, 1883, Arachnida].

The four-times preoccupied nominal genus *Nesis* "Monterosato" Locard, 1899 seems never to have been renamed, and is not included in



Charnière de *Nesis prima* Monts.

Figure 11. Copy of Lamy's figure of the interior of both valves of *Monterosatus primus* (Locard), X 2; original magnification not stated by Lamy.

the Bivalvia volume of the "Treatise on Invertebrate Paleontology" (Keen, 1969). The replacement name *Monterosatus* (gender: masculine) is here proposed for it (type species: *Nesis prima* "Monterosato" Locard, 1899).

Although Lamy (1914: 13) and several earlier authors regarded *Nesis* Monterosato as an available name, where first published *Nesis* satisfies none of the requirements of the International Code of Zoological Nomenclature, and can only be construed as a *nomen nudum* (Monterosato, 1875: 4). *Nesis prima*, the single species included in the genus later in the original work (Monterosato, 1875: 17), is a *nomen nudum* also. The same species was listed in two later works by Monterosato (1878: 73; 1884: 27) but was not made available. As noted by Pallary (1900: 408), at the next subsequent reference Locard (1899: 135-6) published the first description of the genus and species, and thus rendered them available. Thus Locard must be considered the author of the genus and species. Monterosato (in Sacco, 1901: 21) later published a description of *Nesis secunda* from the Italian Pliocene, and (Sacco, 1901: pl. 29, figs. 47-50) gave clear photographs of both *Nesis prima* Locard and *Nesis secunda* Monterosato. Pallary (1900: 408) noted that *Nesis prima* is a reasonably common Mediterranean shell.

The best figure of the interior of "*Nesis*" *prima*, based on "type" material of "*Nesis prima* Monterosato" and showing the hinge features clearly, is the drawing published by Lamy (1914: 13), and repeated here (Fig. 11). It shows a minute shell with large muscle scars, and a broad pallial line that lacks any trace of a posterior sinus. Thus the genus *Monterosatus* is here tentatively referred to the Davilinae. It bears a most unusual dorsally-projecting posterior hinge structure, interpreted by Lamy (1914) to be a ligamental nymph. If the apparent mactracean resilifer is correctly interpreted, the genus can be placed in no other family but the Mesodesmatidae, but shells and, preferably, animals should be re-examined before such a position can be accepted with confidence.

In summary, the valid names of the species of *Monterosatus* are: *Monterosatus primus* (Locard, 1899); *Monterosatus secundus* (Monterosato in Sacco, 1901).

Subfamily Erviliinae Dall, 1895

Genus *Ervilia* Turton, 1822

- 1822 *Ervilia* Turton, *Conchylia Insularum Britannicarum* (2): 55. Type species (by monotypy): *Mya nitens* Montagu, 1808, Recent, West Indies (Europe?).

A widespread genus containing many species of small, generalised form. It bears fine but well-marked radial sculpture which, if present, is usually limited to the posterior part of the shell.

Subgenus *Spondervilia* Iredale, 1930

- 1930 *Spondervilia* Iredale, *Rec. Aust. Mus.*, 17: 402. Type species (by original designation): *Ervilia australis* Angas, 1877, Recent, eastern Australia.

As pointed out by Dall, Bartsch and Rehder (1938: 170), *Spondervilia* differs from *Ervilia* mainly by bearing radial sculpture all over, rather than merely on the posterior end. They reduced *Spondervilia* to a subgenus of *Ervilia*.

Genus *Argyrodonax* Dall, 1911

1911. *Argyrodonax* Dall, *Nautilus*, 25: 85. Type species (by original designation): *Argyrodonax haycocki* Dall, 1911, Recent, Bermuda.

This genus still seems to be known only by the type species, a minute (5.5 x 4.5 mm) shell from Bermuda. Dall (1911) compared it with *Anapella* (Davilinae) but stated that the pallial sinus is "large and deep". Thus Keen (1969: N610) referred *Argyrodonax* to the Erviliinae. If the genus is correctly referred to the Mesodesmatidae (Dall also compared it with *Cumingia*), the Erviliinae would appear to be the better location for it.

Keen (1969: N610) stated that the type was selected by monotypy, but Dall (1911: 85) clearly named *Argyrodonax haycocki* as type.

Genus *Coecella* Gray, 1853

1853. *Coecella* J. E. Gray, *Ann. Mag. Nat. Hist.*, (2), 11: 43. Type species (by monotypy): *Coecella horsfieldii* Gray, 1853, Recent, Indo-West Pacific.

In the original paper, Gray (1853: 43) spelled *Coecella* with a digraph. The "o" and "e" are joined together, disguising the shape of the "o"; all subsequent workers have interpreted the spelling as *Caecella*. As pointed out by Mr D. Heppell, examination of the "ae" digraphs at the ends of family names throughout Gray's paper, including two on p. 43, shows that *Coecella* is spelled with an "oe" digraph rather than an "ae". Thus the correct original spelling, *Coecella*, is used in this paper.

Coecella was placed in the Mactridae by Gray (1853: 43), but Dall (1898: 914) pointed out that it was closely related to *Ervilia*. Lamy (1914: 10) considered that *Coecella* was based on little more than large species of *Ervilia*.

If my conclusions on combined genus and species descriptions are not accepted, no type species will have been validly designated for *Coecella*.

No-one has ever designated any species but "*C. horsfieldii* Gray" as type of *Coecella*, but strictly speaking, as this would be unavailable if my conclusions are not accepted, another species must be designated. Accordingly, I here designate *Coecella horsfieldii* Deshayes, 1854 as type species of *Coecella* Gray, 1843.

Genus *Rochefortina* Dall, 1924

1924. *Rochefortina* Dall, *Proc. Biol. Soc. Wash.*, 37: 88. Type species (by original designation): *Rochefortia* (*Rochefortina*) *semele* Dall, 1924 (= *Ervilia sandwichensis* E. A. Smith, 1885), Recent, Hawaii.

Dall (1924) erected *Rochefortina* as a subgenus of *Rochefortia* (Montacutidae). Later Dall, Bartsch and Rehder (1938: 169) pointed out that the type species was a junior synonym of *Ervilia sandwichensis* E. A. Smith, 1885, and that *Rochefortina* was a genus of the Mesodesmatidae. The type species is very similar to *Ervilia* in most respects, and *Rochefortina* evidently belongs in the subfamily *Erviliinae*.

Family Myadesmatidae Clark, 1922

(*nom. correct.* herein *pro* Myadesmidae Clarke, 1922)

Genus *Myadesma* Clark, 1922

1922. *Myadesma* Clark, *Univ. Calif. Pubs., Bull. Dep. Geol. Sci.*, 14 (4): 116. Type species (by original designation): *Myadesma dalli* Clark, 1922, Oligocene, Vancouver Id.

Clark (1922) erected *Myadesma* and the family "Myadesmidae" for three species previously thought to belong in *Mesodesma*. The species are similar to *Mesodesma* in their trigonal shape with beaks near the posterior end, in having a well-marked shallow pallial sinus, in having anteriorly directed resilifers, and in having prominent, smooth lateral teeth like those of *Paphies* (s.str.) and *Mesodesma*; also, "tooth-like structures" alongside the resilifers described by Clark appear to be better interpreted as cardinal teeth. Clark referred the family to the "Anomalodesmacea" on the basis of the resemblance of the resilifers to those of the Myidae; the resilifer of the right valve protrudes strongly beyond the plane of the commissure, whereas that of the left valve is sunken, and fused to the valve itself. What was identified as a lithodesma by Clark is sometimes fused to the resilifer of the right valve.

In general features *Myadesma* closely resembles *Mesodesma*, and seems better referred to the Mactracea than to the Myacea. Keen (1969: N610) included *Myadesma* tentatively in the Mesodesmatidae. However, the Mya-like projection of one resilifer and sinking of the other precludes inclusion in that family, and the genus is here retained in its own family, in the Mactracea. Until the shell structure and hinge details are adequately known, this must remain a tentative assignment.

Mesodesmatidae

SYNOPSIS OF CLASSIFICATION OF THE MESODESMATIDAE

The tendency to form geographic genera and subgenera is unusually well marked in this family, particularly in the subgenera of *Paphies*.

Family Mesodesmatidae Gray, 1840

Subfamily Mesodesmatinae Gray, 1840

Genus *Atactodea* Dall, 1895; Indo-Pacific;

? Genus *Ceroniola* Wilckens, 1904; Upper Cretaceous, South America;

Genus *Donacilla* de Blainville, 1819; Mediterranean;

Genus *Mactropsis* Conrad, 1854; Eocene, south-eastern U.S.A.;

Genus *Paphies* Lesson, [1831];

Subgenus *Amesodesma* Iredale, 1930; southern Australia;

Subgenus *Ceronia* Gray, 1853; eastern North America;

Subgenus *Mesodesma* Deshayes, [1832]; New Zealand and South America;

Subgenus *Paphies* s.str.; New Zealand.

Subfamily Davilinae Dall, 1895

Genus *Anapella* Dall, 1895; southern Australia;

Genus *Davila* Gray, 1853; Indo-Pacific;

Genus *Monterosatus* nom. nov.; Mediterranean.

Subfamily Erviliinae Dall, 1895

Genus *Argyrodonax* Dall, 1911; Bermuda;

Genus *Coecella* Gray, 1853; Indo-Pacific;

Genus *Ervilia* Turton, 1822; Cosmopolitan;

Subgenus *Spondervilia* Iredale, 1930, Indo-Pacific;

Genus *Rochefortina* Dall, 1924; Hawaii.

? Family Myadesmatidae Clark, 1922

Genus *Myadesma* Clark, 1922; Oligocene of Western Canada.

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